

Abundance, growth rate and parasitism of *Brevicoryne brassicae* and *Myzus persicae* (Homoptera: Aphididae) on broccoli grown in living mulches

Michael J. Costello*, Miguel A. Altieri

Laboratory of Biological Control, University of California, Berkeley, CA 94706, USA

Abstract

In 1990 and 1991, populations of the cabbage aphid, *Brevicoryne brassicae*, and the green peach aphid, *Myzus persicae*, were monitored on broccoli interplanted with three leguminous cover crops (the living mulches) and compared with broccoli without cover crop (clean cultivation). The cover crops used were white clover (*Trifolium repens* L.), strawberry clover (*Trifolium fragiferum* L.) and a mixture of birdsfoot trefoil (*Lotus corniculatus* L.) and red clover (*Trifolium pratense* L.). Fertilizer was applied as compost or synthetic fertilizer crossed with cropping system regime. *Brevicoryne brassicae* can reach pest status in *Brassica* cropping systems, whereas *M. persicae* is generally innocuous. Both aphids are attacked by the parasitoid *Diaeretiella rapae*. Seasonal aphid abundance, parasitism and population growth rates were analyzed.

No significant effect of fertilizer was found for any of the parameters analyzed. The living mulches had lower aphid populations overall, although differences with clean cultivation were greatest early in the season for *M. persicae* and diminished over time. No effect of cropping system on population growth rate was seen for *Brevicoryne brassicae*, but for *M. persicae* growth rates were higher in living mulches compared with clean cultivation. Parasitism was highest on clean cultivated broccoli for both aphid species in 1990 and for *M. persicae* in 1991, but no differences were found for *Brevicoryne brassicae* in 1991. This suggests that differential population growth rates and parasitism seen for *M. persicae* are a result of inhibition of *D. rapae* in the living mulches. Possible reasons for differences in parasitism between the two aphid species in living mulches and clean cultivation are discussed.

Keywords: *Brevicoryne brassicae*; *Myzus persicae*

1. Introduction

Increasing vegetational diversity in agroecosystems, either by intercropping or by interplanting a crop with non-crop vegetation, has

frequently been tested as a method of insect pest population control, but with variable results (see recent reviews by Russell, 1989; Andow, 1991). This variability can in part be attributed to differences in natural enemy feeding ranges (generalist vs. specialist) and methods of host finding (visual, olfactory or random), as well as differences in herbivore response to changes in host plant quality in diverse plantings.

* Corresponding author at: Laboratory of Biological Control, UC Berkeley, Kearney Agricultural Center, 9240 S. Riverbend Ave., Parlier, CA 93648, USA.

The enemies hypothesis states that populations of insect natural enemies will be more abundant in vegetationally diverse cropping systems because of the variety of microhabitats or food resources (Root, 1973). However, results from studies which have tested this hypothesis with respect to parasitism have varied. Parasitism in vegetationally diverse cropping systems has been enhanced (Letourneau, 1987; Horn, 1988), decreased (Smith, 1976b; Andow and Risch, 1987) or has shown no change (Altieri, 1984; Letourneau, 1990) compared with crop monocultures. Sheehan (1986) argued that vegetational diversity may interfere with specialist parasitoid searching abilities because of masking of chemical cues used to orient to their hosts or inability to recognize patch boundaries. Andow (1991) suggested that the increased plant structural complexity (the way that plant surface area is connected together, see Andow and Prokrym, 1990) inherent in diversified cropping systems may interfere with parasitoid host-finding. In addition, vegetational diversity may cause parasitoids which search randomly to spend more time on vegetation which does not harbor their insect hosts, which would lead to less frequent host encounters and/or decreased patch tenure times.

In addition to effects on natural enemies, vegetational diversity can affect plant quality. When plant species are mixed there is a high probability of changes in host plant quality because of increased competition for resources such as light, nutrients and water (Andow, 1991). This can lead to higher rates of herbivore emigration (Kareiva, 1982) or lower rates of herbivore population growth (Finch, 1988) compared with single species plantings.

Aphid populations on annual crops have been consistently lowered by interplanting with weedy vegetation or cover crops (Dempster and Coaker, 1974; O'Donnell and Coaker, 1975; Altieri et al., 1985; Andow et al., 1986; Horn, 1988; Cartwright et al., 1990). The lower numbers of aphids in these systems is often attributed to a decrease in numbers of immigrant alates, which are known to be affected by crop background (Costello, 1995). However, less is known about

the effects of interplanted non-crop vegetation on the post-colonization development of aphids, which is affected by biotic mortality agents and host plant quality. Studies of the cabbage aphid, *Brevicoryne brassicae* (L.), in *Brassica* cropping systems have found variable rates of parasitism in interplantings compared with clean cultivated monocultures (Smith, 1976b; Altieri et al., 1985; Horn, 1988; Kloen and Altieri, 1990). Main crop growth parameters are often lower when interplanting with non-crop vegetation (Dempster and Coaker, 1974; O'Donnell and Coaker, 1975; Altieri et al., 1985; Andow et al., 1986; Horn, 1988), making it difficult to determine whether effects seen on aphid populations are the results of parasitism or changes in plant quality.

Brassica crops are cultivated year round in the moderate climatic zones of the central California coast, and are colonized by *Brevicoryne brassicae* and the green peach aphid, *Myzus persicae* (Sulzer). *Brevicoryne brassicae* is a specialist on the Brassicaceae and prefers feeding on younger plant tissues, which makes it the aphid of economic importance on broccoli as it can move into the developing floral buds and render the head unmarketable. *Myzus persicae* is a generalist which feeds on a wide range of plants in several families, but is generally not of economic importance on *Brassica* crops. Both aphids are attacked by the parasitoid *Diaeretiella rapae* M'Intosh (Hymenoptera: Braconidae), which tends to specialize on crucifer-feeding aphids, but has also been reported attacking numerous other aphids species on a range of plant families (Sheehan and Shelton, 1989a).

At the University of California Agricultural Experiment Station in Albany, early-season populations of *Brevicoryne brassicae* and *M. persicae* on broccoli were lower when interplanted with clover (a living mulch) compared with clean cultivation (Costello, 1992). However, by season's end no differences in aphid abundance remained among treatments, suggesting that aphid growth rates in living mulches were higher. Further studies were therefore undertaken at a site in the Salinas Valley, California, to determine whether aphid abundance followed a similar pattern and if so, to identify the mechanisms in-

volved. Included in the study was a comparison of organic vs. conventional fertilizers to ascertain if this had any effect on host plant quality and, consequently, aphid abundance.

2. Materials and methods

Experiments were conducted at the Rural Development Center farm from September to December 1990 and May to July 1991. The experiment was a 4×2 factorial, in a randomized complete block/split plot design, with blocks replicated four times and plot size $10 \text{ m} \times 10 \text{ m}$. The main plot factor consisted of four cropping system levels: three cover crops interplanted with broccoli (the living mulches, hereafter denoted LM) and a clean cultivated (no cover crop) control. The cover crops used were white clover (*Trifolium repens* L.), strawberry clover (*Trifolium fragiferum* L. cv. 'O'Connors') and a mixture of birdsfoot trefoil (*Lotus corniculatus* L. cv. 'Kalo') and red clover (*Trifolium praetense* L.). Two fertilizer levels comprised the sub-plot factor: synthetic fertilizer or chicken manure/rice hull compost. Nitrogen availability in the plots given compost was low, which meant that plots given compost had lower crop growth parameters than those given synthetic fertilizer (Costello, 1994). Crop growth, however, was not negatively affected in the living mulches (Costello, 1994). Broccoli was transplanted at an intra-row spacing of 22 cm with 0.6 m between rows (approximately $72\,000 \text{ plants ha}^{-2}$). Cover crops in the living mulch plots covered 83% of the inter-row area. Further methodology is described in Costello (1994).

Aphids were sampled by taking 50 broccoli leaves from 50 separate plants in each sub-plot, excluding the two outer rows. Sampling was stratified according to plant stratum (upper, $n=15$; middle, $n=25$; lower, $n=10$; subplot row, $n=10$ per row). Samples were taken every 2 weeks in 1990 and every 10 days in 1991. Sampling dates are presented as days after planting (DAP).

Aphids were heat-extracted using a combination of the methods described by Hughes (1963)

and Pielou (1961). Aphids and mummies (parasitized fourth instar and adult aphids) were segregated according to species and counted by instar using the keys of Raworth et al. (1984) and Dodd (1976). Third instar aphids containing parasitoids which had undergone considerable development but which had not yet mummified were noted and scored as parasitized.

2.1. Statistical analysis

Aphid abundance data were \log_{10} transformed and analyzed by repeated measures ANOVA (Statistical Analysis Systems Institute Inc. (SAS Institute Inc.), 1988), using leaf area as a covariate to partition any variation due to plant size. If plant size was found not to be significant ($P > 0.05$), then the data were reanalyzed without the covariate. The mean aphid abundance from each living mulch was compared with clean cultivation using orthogonal contrasts. No contrast was declared significant unless the overall ANOVA was significant at $P < 0.05$.

Parasitism was determined as: $\% \text{ parasitism} = \text{total parasitized aphids (instars III-IV and apterous adults)} \times 100 / (\text{parasitized and non-parasitized aphids (instars III-IV and apterous adults)})$. Parasitism values (those with zero aphid counts removed) were arcsin transformed and analyzed by ANOVA (PROC GLM, SAS Institute Inc., 1988), averaging across sampling dates for each treatment. Means were separated by Tukey's honestly significant difference (HSD).

Aphid population growth rates (r —the \log_e aphids per sample per aphid instar period) were estimated using the method of Hughes (1963) for observed rates of increase. Values of r were analyzed by ANOVA (PROC GLM, SAS Institute Inc., 1988), averaging across sampling dates for each treatment, with means separated by Tukey's HSD.

Determination of broccoli leaf nitrate-nitrogen is described in Costello (1994). Linear regression analysis was used to determine the association between aphid population growth rates and broccoli leaf nitrate-nitrogen, using samples from strawberry clover LM and clean cultivation

treatments in 1991 (PROC GLM, SAS Institute Inc., 1988).

3. Results and discussion

3.1. Effects of fertilizer on aphid abundance

Differences in aphid abundance between fertilizer types did not meet the 5% level of significance in either season (Table 1), although numbers of *M. persicae* were marginally higher ($P=0.08$) in compost (season-wide mean of 0.31 ± 0.07 per leaf) vs. synthetic fertilizer (0.25 ± 0.08 per leaf) in 1990. There was no interaction between fertilizer and cropping system in either season. Regression analysis did not reveal any relationships between population growth rates (r) and leaf nitrate-nitrogen for either aphid species ($F=0.75$, d.f. = 1108, $P=0.39$, $R^2=0.00$ for treatments and aphid species combined). This lack of response to fertility was unexpected, given the studies showing a relationship between nitrogen level and aphid growth parameters (Van Emden, 1966; Van Emden and Bashford, 1969). Leaf nitrate-nitrogen in the synthetically fertilized broccoli was as much as 23 times higher than broccoli fertilized with compost (Costello,

1994). Van Emden and Bashford (1969) found a positive correlation between *M. persicae* and *Brevicoryne brassicae* fecundity and leaf nitrogen (declining at higher levels for *Brevicoryne brassicae*). Jansson and Smilowitz (1986) found that population growth rate for *M. persicae* on potatoes increased with the rate of nitrogen applied and Culliney and Pimentel (1986) found elevated levels of alate aphids (combined *Brevicoryne brassicae*, *M. persicae* and *Lipaphis erysimi* (Kaltenbach)) on unfertilized (nutrient stressed) collards. It may be that nitrogen levels in the present study were not extreme enough to influence the growth and reproductive rate of the aphids on the leaves. However, infestation of harvested broccoli heads by *Brevicoryne brassicae* was greatest in the clean cultivated/compost treatment (Costello, 1994), suggesting that nitrogen stress may have more of an effect on its growth and reproduction in the broccoli flower buds. Fertilizer did not have an effect on initial colonization rates (Costello, 1995).

3.2. Effects of cover crop on aphid abundance

Early season aphid populations were consistently lower on broccoli in all living mulches compared with clean cultivation (Figs. 1 and 2),

Table 1

F-test and corresponding probability (P) values for effects of cropping system, fertilizer, sampling date and their interactions with repeated measures analysis of variance for log transformed numbers of apterous aphids ($\log_{10}(n+1)$) per plant

Source of variation	d.f.	<i>M. persicae</i>				<i>B. brassicae</i>			
		1990		1991		1990		1991	
		F	P	F	P	F	P	F	P
Block	3	—	—	—	—	—	—	—	—
Cropping system (CS)	3	62.6	0.0001	30.4	0.0001	15.4	0.0007	13.2	0.001
Error a	9								
Fertilizer (F)	1	3.5	0.08	0.0	0.89	1.6	0.22	1.3	0.28
CS×F	3	1.8	0.20	0.3	0.82	0.2	0.87	0.0	0.97
Error b	12								
Date (D)	2	6.4	0.006	26.2	0.0001	0.0	0.95	17.1	0.0001
D×CS	6	1.1	0.41	4.3	0.0001	2.2	0.08	1.9	0.057
D×F	2	0.0	0.98	0.8	0.52	2.0	0.14	1.7	0.16
D×CS×F	6	0.8	0.57	0.5	0.88	0.7	0.67	1.0	0.40
Error c	48								

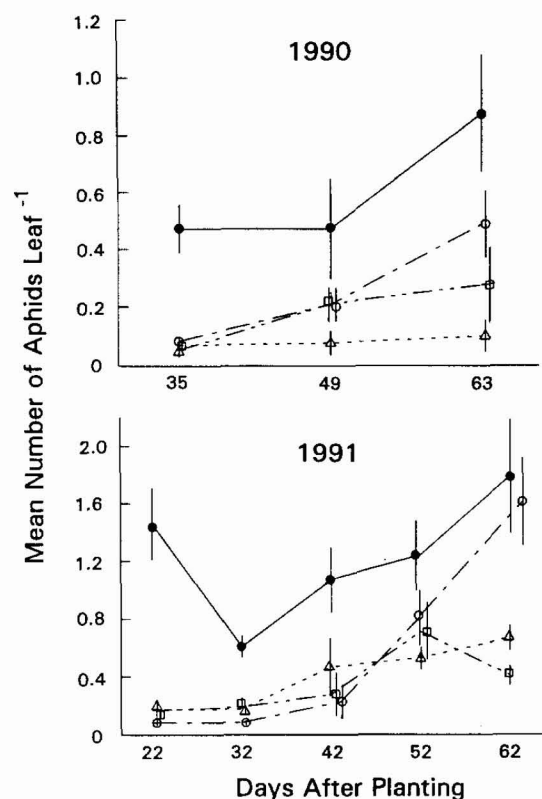


Fig. 1. Mean apterous *M. persicae* abundance on broccoli in living mulches (LM) and under clean cultivation, in 1990 and 1991. Error bars are standard error of the mean. ○, white clover LM; △, strawberry clover LM; □, trefoil/red clover LM; ●, clean cultivation.

which was the result of reduced alate aphid colonization (Costello, 1995).

All living mulches significantly reduced *M. persicae* abundance in both 1990 and 1991 compared with clean cultivation (Fig. 1; Table 2). In addition, there was significant date by cropping system interaction in 1991; compared with clean cultivation, numbers were significantly lower on 22, 32, 42 and 62 DAP in strawberry clover LM (contrast $F=52.13, 63.46, 11.61$, and 8.18 , respectively; d.f. = 1, 12; $P=0.0001, 0.0001, 0.008$ and 0.02 , respectively) and trefoil/red clover LM (contrast $F=53.25, 59.13, 18.54$ and 15.38 , respectively; d.f. = 1, 12; $P=0.0001, 0.0001, 0.002, 0.004$, respectively) but not on 52 DAP. The population in white clover LM was lower on 22, 32 and 42 DAP (contrast $F=65.54, 99.57, 21.10$, respectively; d.f. = 1, 12; $P=0.0001, 0.0001$ and 0.0013 , respectively), but not on 52 or 62 DAP.

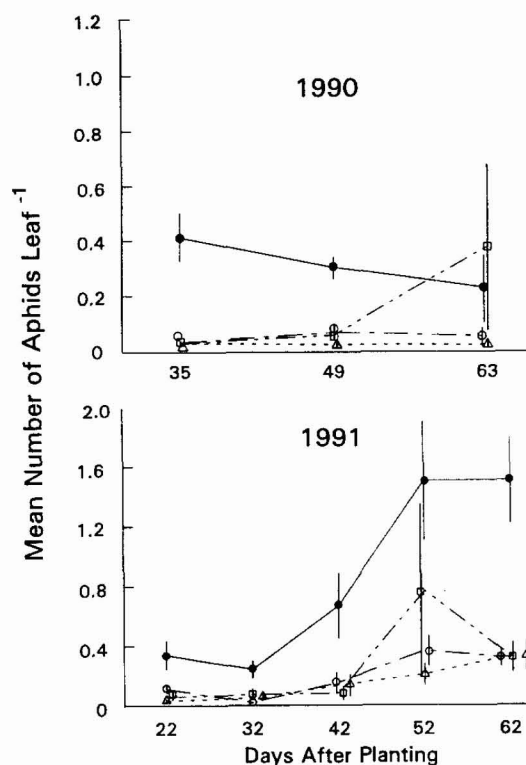


Fig. 2. Mean apterous *Brevicoryne brassicae* abundance on broccoli in living mulches (LM) and under clean cultivation, in 1990 and 1991. Error bars are standard error of the mean. ○, white clover LM; △, strawberry clover LM; □, trefoil/red clover LM; ●, clean cultivation.

Aphid numbers were 82%, 56% and 44% lower in white clover LM than clean cultivation on the three sampling dates, respectively, in 1990, and 95%, 86%, 78%, 34% and 10% lower on the five sampling dates in 1991, respectively. This pattern of diminishing differences over the course of the season is similar to that seen for combined populations of *M. persicae* and *Brevicoryne brassicae* on broccoli in clover living mulches (Costello, 1992), and for *M. persicae* on bell peppers in rye living mulches (Cartwright et al., 1990). The population of *M. persicae* in strawberry clover LM was most consistently lower than in clean cultivation in 1990 (85%, 84% and 88% on the sampling dates, respectively), but in 1991 differences narrowed somewhat between early-season (88% lower in strawberry clover LM) and mid-to late-season (57–63% lower) in 1991.

Living mulches also significantly reduced *Brevicoryne brassicae* abundance in both 1990

Table 2

Estimated season-wide population growth rates (r —the \log_e aphids per sample per instar period \pm SEM) for *Myzus persicae* and *Brevicoryne brassicae* in living mulches (LM) and clean cultivation

Season	Aphid sp.	Cropping system	r (\pm SEM)	n
1990	<i>M. persicae</i>	White clover LM	1.20(0.08)a	44
		Trefoil/red clover LM	1.13(0.13)ab	30
		Strawberry clover LM	0.92(0.14)ab	33
		Clean cultivation	0.86(0.10)b	44
	<i>B. brassicae</i>	White clover LM	0.75(0.14)a	25
		Trefoil/red clover LM	0.85(0.15)a	31
		Strawberry clover LM	0.85(0.18)a	21
		Clean cultivation	0.78(0.08)a	48
1991	<i>M. persicae</i>	White clover LM	1.45(0.11)a	93
		Trefoil/red clover LM	1.26(0.10)a	92
		Strawberry clover LM	1.33(0.09)a	91
		Clean cultivation	0.97(0.08)b	95
	<i>B. brassicae</i>	White clover LM	1.25(0.13)a	73
		Trefoil/red clover LM	1.37(0.14)a	67
		Strawberry clover LM	1.39(0.14)a	66
		Clean cultivation	1.33(0.09)a	92

Means within a group followed by the same letter are not significantly different ($P > 0.05$).

and 1991 compared with clean cultivation, with no interaction (Fig. 2; Table 2). The population of *Brevicoryne brassicae* in white clover LM displayed a weak pattern of decreasing differences with clean cultivation in 1990 (numbers lower by 92%, 81% and 78% on 35, 49 and 63 DAP, respectively) but in 1991 no such consistent diminution over time was seen (differences of 67% on 22 DAP and 79% on 62 DAP). The sharp rise in numbers of *Brevicoryne brassicae* in trefoil/red clover LM on 63 DAP in 1990 was due to a very high count on just one leaf. Numbers of *Brevicoryne brassicae* in 1990 were most consistently lower on strawberry clover LM compared to clean cultivation (94%, 93% and 92% on the three sampling dates, respectively).

3.3. Population growth rates

The rate of population increase of *Brevicoryne brassicae* did not differ between any of the living mulches and clean cultivation in either season (Table 2). However, r for *M. persicae* was significantly greater in white clover LM compared with clean cultivation in 1990 (Table 2), and was

greater for all living mulches vs. clean cultivation in 1991 (Table 2). This finding corresponds with that of Helenius (1989), who observed higher rates of increase for the bird cherry/oat aphid (*Rhopalosiphum padi* L.) on oats interplanted with field beans compared with a pure stand of oats. The higher r values for *M. persicae* in the white clover living mulch compared with clean cultivation corresponds to the observed patterns of abundance, i.e. late-season populations levels approaching those found in clean cultivation. Growth rates in the other living mulches, although statistically equivalent with white clover LM on a season-wide basis, did not result in aphid densities approaching that in clean cultivation at the end of the season.

3.4. Parasitism

Percent parasitism in 1990 for both aphid species was significantly higher in clean cultivation compared with all living mulches (Table 3). No parasitism was recorded in strawberry clover LM. In 1991 parasitism in clean cultivation was significantly greater compared with all living

Table 3

Season-wide percent parasitism (\pm SEM) of *Myzus persicae* and *Brevicoryne brassicae* in living mulches (LM) and clean cultivation

Season	Aphid sp.	Cropping system	% parasitism	n
1990	<i>M. persicae</i>	White clover LM	1.34(0.95)a	31
		Trefoil/red clover LM	3.03(2.09)a	22
		Strawberry clover LM	0.00(0.00)a	18
		Clean cultivation	10.05(2.18)b	39
	<i>B. brassicae</i>	White clover LM	3.33(3.33)a	6
		Trefoil/red clover LM	7.20(3.29)a	16
		Strawberry clover LM	0.00(0.00)a	12
		Clean cultivation	17.83(2.37)b	45
1991	<i>M. persicae</i>	White clover LM	2.54(1.20)a	53
		Trefoil/red clover LM	2.27(0.97)a	50
		Strawberry clover LM	2.83(1.06)a	55
		Clean cultivation	13.84(1.49)b	83
	<i>B. brassicae</i>	White clover LM	12.19(2.27)a	47
		Trefoil/red clover LM	11.35(2.29)a	42
		Strawberry clover LM	13.04(2.67)a	33
		Clean cultivation	15.38(1.45)a	84

Means within a group followed by the same letter are not significantly different ($P > 0.05$).

mulches for *M. persicae*, but no differences were found between clean cultivation and any of the living mulches for *Brevicoryne brassicae* (Table 3).

These results show a trend toward lower parasitism by *D. rapae* where crops are associated with non-crop vegetation and support the hypothesis that vegetational diversity can provide a barrier to parasitoid searching ability (Sheehan, 1986; Andow and Risch, 1987). Given the evidence that *D. rapae* is attracted to host plant odor (Read et al., 1970; Akinlosotu, 1977; Sheehan and Shelton, 1989b), it seems likely that the barrier in the living mulches was an olfactory one, though the contribution of increased plant structural complexity cannot be ruled out. Reduced parasitism in living mulches was consistent on *M. persicae*, but was found on *Brevicoryne brassicae* only in 1990. Results from previous studies with *Brevicoryne brassicae* have also been mixed. Smith (1976b) found lower parasitism by *D. rapae* on *Brevicoryne brassicae* in a weedy Brussels sprouts compared with monoculture in only 1 of 3 years, whereas Altieri et al. (1985) and Horn (1988) found higher parasitism in weedy vs.

monoculture *Brassica* crops. No change in parasitism of *Brevicoryne brassicae* was found when interplanted vegetation was fava bean (*Vicia fava* L.) (Altieri, 1984), vetch (*Vicia sativa* L.) (Altieri et al., 1985), or mustard (*Brassica hirta* Moench; Kloen and Altieri, 1990). It is possible that the non-crop vegetation weeds in some of these studies provided a nectar source which contributed to increased *D. rapae* longevity, tenure time and/or fecundity. Evidence of visitation to nectiferous plants has been found for some aphidiines (braconid parasitoids of aphids), including *D. rapae* (Jervis et al., 1993), but only if patch tenure time were increased would the availability of nectar offset any olfactorial or plant structural inhibition of parasitoid searching ability. However, when aphids are the primary pest, the presence of nectiferous plantings may be of little consequence because of the availability of aphid-produced honeydew as a food source for aphidiines (N.J. Mills, personal communication, 1994).

The evidence suggests that the lower rates of parasitism in the living mulches contributed to higher *M. persicae* population growth rates in

1991. Differential rates of parasitism, however, do not consistently explain differences in r values in 1990. In that season the population of *M. persicae* in white clover LM was the only one with a significantly higher r value compared with clean cultivation, whereas all living mulches had lower rates of parasitism than clean cultivation. In addition, r did not differ between any of the living mulches and clean cultivation for *Brevicoryne brassicae*, but percent parasitism was significantly higher under clean cultivation compared with all living mulches. These inconsistencies may be due to the low number of samples with aphids or mummies in 1990 compared with 1991 (Tables 2 and 3).

It cannot be ruled out that parasitism in these studies is merely a response to aphid density. In both seasons *M. persicae* densities were higher in the clean cultivated plots, which had consistently higher rates of parasitism compared with living mulches. Densities of *Brevicoryne brassicae* in living mulches were very low in 1990, when parasitism was lower compared with clean cultivation. However, the higher rates of parasitism found by Smith (1976b) in a Brussels sprouts monoculture were at equivalent aphid densities as the weedy Brussels sprouts (Smith, 1976a), and Helenius (1990) found a higher rate of parasitism in an oat monoculture despite finding a higher aphid density in mixtures of oats and fava beans. Thus, further studies on parasitism with control of aphid density would be helpful in separating the effects of host density from crop diversity.

It is uncertain why, in 1991, parasitism was negatively affected in the living mulches for *M. persicae* but not *Brevicoryne brassicae*, given that the same parasite attacks both aphid species. This contradicts the findings of Horn (1988), who found no differences in parasitism by *D. rapae* on *Brevicoryne brassicae* and *M. persicae*. One possible explanation lies in the different ways that the aphids distribute themselves on the leaf. *Brevicoryne brassicae* nymphs remain close to their stem mother and therefore populations have an aggregated distribution, whereas *M. persicae* nymphs tend to disperse at birth and maintain a more uniform distribution. It may be that the in-

hibitory effect of the living mulch on parasitoid searching ability caused *D. rapae* to increase tenure time at colonies of *Brevicoryne brassicae* compared with the more widely dispersed *M. persicae*. Interesting, Lopez et al. (1990) found that scattered *Brevicoryne brassicae* are more likely to be attacked by *D. rapae* than *Brevicoryne brassicae* in colonies. Clearly, there is no such preference for scattered *M. persicae* over colonial *Brevicoryne brassicae*. It is also possible that the preference of *D. rapae* for *Brevicoryne brassicae* (Hafez, 1961) played a role in differential parasitism, but it is difficult to see why this preference would be exhibited in the living mulches but not in clean cultivation.

These studies corroborate earlier findings that aphid populations can be lowered on crops grown with interrow vegetation, although this advantage was strongest in the early part of the growing season, and declined thereafter for *M. persicae*. However, because it is *Brevicoryne brassicae* and not *M. persicae* which causes economic damage on *Brassica* crops, the living mulches were successful as a cultural method of pest control, and contributed to lower pest damage levels (see Costello, 1994).

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